

Durham Research Online

Deposited in DRO:

01 April 2016

Version of attached file:

Published Version

Peer-review status of attached file:

Peer-reviewed

Citation for published item:

Tummers, J.S. and Winter, E. and Silva, S. and O'Brien, P. and Jang, M-H. and Lucas, M.C. (2016)
'Evaluating the effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles.', *Ecological engineering*, 91 . pp. 183-194.

Further information on publisher's website:

<http://dx.doi.org/10.1016/j.ecoleng.2016.02.046>

Publisher's copyright statement:

© 2016 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Additional information:

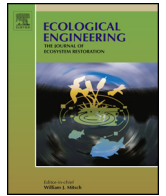
Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in DRO
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full DRO policy](#) for further details.



Evaluating the effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles



Jeroen S. Tummers^{a,*}, Emily Winter^a, Sergio Silva^{a,b,c}, Pat O'Brien^d, Min-Ho Jang^e, Martyn C. Lucas^a

^a School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, UK

^b Department of Zoology and Physical Anthropology, Faculty of Biology, University of Santiago de Compostela, Spain

^c Hydrobiology Station "Encoro do Con", Castroagudín s/n, Vilagarcía de Arousa, Pontevedra, Spain

^d Environment Agency, Coverdale House, York, UK

^e Department of Biology Education, Kongju National University, Kongju, Chungnam, South Korea

ARTICLE INFO

Article history:

Received 7 September 2015

Received in revised form 18 January 2016

Accepted 27 February 2016

Keywords:

Migration

Connectivity

Acoustic telemetry

PIT

Larinier fish pass

ABSTRACT

To help achieve effective longitudinal river connectivity, evaluation of the efficacy of fishway use by upstream-migrating fishes is needed. Larinier super active baffle (SAB) fishways are relatively cheap retrofit fish passes, suitable for low-head barriers, widespread in Europe and the most commonly fitted technical pass in Britain. Their suitability for non-salmonids, however, is poorly quantified. The efficacy of a 15% gradient SAB fishway and effects of flow regime and water temperature were tested for European river lamprey (*Lampetra fluviatilis*) using passive integrated transponder (PIT) and acoustic telemetry at a Crump weir on the River Derwent, Northeast England. In migration season 2013–14, over a wide range of flows, 90.1% of 350 tagged lamprey entered the fishway. One fish (0.3%) of those that entered the pass ascended successfully, even though measured water velocity was within laboratory-measured performance conditions for this species. Of 29 acoustic-tagged lamprey that visited the weir over the same period, four (13.8%) ascended it directly, during elevated flows. These data suggest that high turbulence and/or the physical characteristics of baffles may inhibit lamprey ascent of the pass. In migration season 2014–15, we tested the effect of adding studded modular plastic tiles adjacent to the fishway wall, employing PIT antennas separately interrogating the entrance and exit of each of the main fishway and tile routes. 85.8% (169) of 197 tagged lamprey entered the fishway, of which 72/169 (42.6%) entered the tile entrance. Passage efficiency of entrants was 7.1% (12/169), all of which used the tiled route. Reduced local flow velocity in combination with increased availability of resting habitat within the tiles may have facilitated increased passage. Although fishway passage efficiency increased after placement of the modular tiles, it remained half that measured for direct weir passage, both of which are inadequate for connectivity restoration. Quantitative tests of studded tiles placed on the sloping downstream weir face by comparison to control conditions may be more effective and are needed. This study demonstrates the importance of carrying out full-scale field tests to supplement possible solutions developed under laboratory conditions.

© 2016 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Globally, ca. 45 000 large dams, exceeding 15 m, were built during the 20th century (World Commission on Dams, 2000). Although considered to be less of an impediment to migratory fish, smaller

engineered structures such as low-head dams and weirs are probably two to four orders of magnitude more abundant than large dams (Lucas et al., 2009). Although these smaller structures may not form absolute barriers, their cumulative negative impacts can be severe, whereby longitudinal connectivity within river systems is often dramatically reduced, flow and sediment regimes are altered (Nilsson et al., 2005; Xu and Milliman, 2009) and channel morphology, vegetation and invertebrate communities are changed (Boon, 1988; Gordon and Meentemeyer, 2006). Direct consequences for

* Corresponding author.

E-mail address: j.s.tummers@durham.ac.uk (J.S. Tummers).

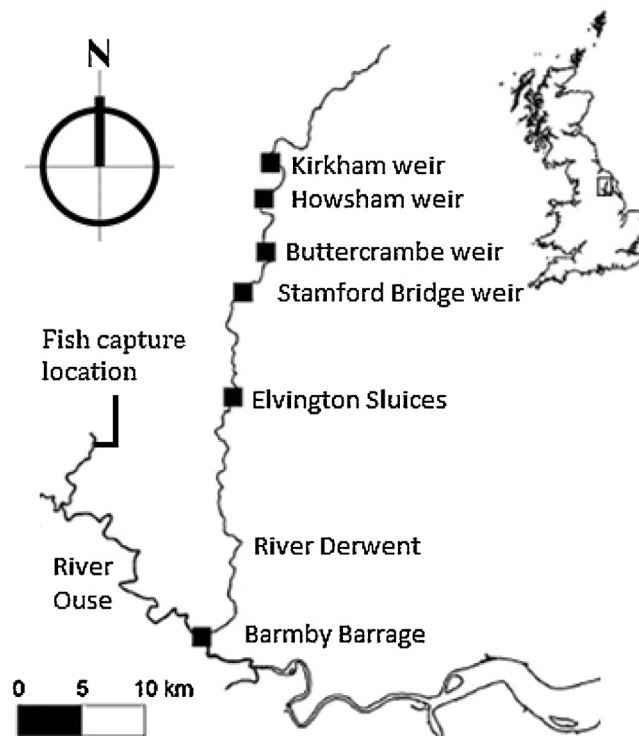


Fig. 1. Location of Buttercrambe weir relative to other obstructions on the lower Derwent and, inset, the study area within Britain. Location of fish capture (on the Ouse) is marked. Fish were released 160 m (solely PIT-tagged) or 620 m (PIT + acoustic tagged) downstream of Buttercrambe weir (on the Derwent).

fish include the loss of, or reduced access to, critical habitat (Cooke et al., 2005; Lucas et al., 2009; Pess et al., 2008), fragmentation and isolation of populations (Baras and Lucas, 2001; McLaughlin et al., 2006) and delayed migration (Caudill et al., 2007; Lucas and Frear, 1997). As a result, fish dependent on natural migration and dispersal between key habitats are often affected (Yoshiyama et al., 1998; Feunteun, 2002) and subsequent population declines (Nelson et al., 2002; Dekker et al., 2007) or, ultimately, population extinctions (Baras and Lucas, 2001; Zabel and Williams, 2002) have been reported.

In order to counter the impacts of obstructions to longitudinal connectivity in river systems, several mitigation measures have been used, including the construction of fish passes (Clay, 1995; Larinier et al., 2002; Larinier and Marmulla, 2004). Technical and nature-like fish passes (Katopodis and Williams, 2011), have the potential to alleviate impoundment effects and facilitate passage for a range of species (Bunt et al., 2012; Clay, 1995; Gough et al., 2012). However, fish passes are often designed to favour conditions for economically important, migration-dependent strongly-swimming species such as salmonids (Larinier and Marmulla, 2004; Williams et al., 2012). Fish passes often perform poorly for other taxonomic groups (Bunt et al., 2012; Cooke et al., 2005; Lucas et al., 1999, 2000; Noonan et al., 2012). Hydraulic conditions, such as flow velocity and turbulence, are critical to the performance of fish passes, both within the pass and at the tail-race (Larinier et al., 2002). For fishways, attraction to the entrance is influenced by the amount and velocity of flow leaving the fish pass, but is also dependent on migratory behaviour and swimming capabilities of fish species, while passage is reliant on hydraulic conditions such as flow velocity and shear stress and swimming ability (Kemp, 2012; Williams et al., 2012). If passage of a broad range of fish species is to be facilitated, consideration of different swimming modes, swimming capabilities (Noonan et al., 2012), behaviour (Kemp, 2012) and life history stages (Baras and Lucas, 2001) are essential criteria.

Lampreys have been widely affected by the impacts of river damming and habitat modification (Close et al., 2002; Mateus et al., 2012; Renaud, 1997) but this group of fishes has been afforded little consideration until recently in terms of upstream passage requirements (Noonan et al., 2012). Indeed, the emphasis had been on preventing passage of non-native sea lamprey *Petromyzon marinus* in the Laurentian Great Lakes (Hunn and Youngs, 1980). Many populations of highly migratory, anadromous lamprey species have declined dramatically throughout their native ranges (Renaud, 1997), including the European river lamprey *Lampetra fluviatilis* (Aronsuu et al., 2015; Lucas et al., 2009; Tuunainen et al., 1980). This species is now widely regarded as endangered throughout large parts of Europe (Mateus et al., 2012; Thiel et al., 2009) and receives protection in designated Natura 2000 sites under the EC Habitats Directive (EC, 1992). The river lamprey is dependent on functional connectivity between key habitats to complete its life cycle, which includes upstream migration of adults between late autumn and spring, when spawning occurs (Hardisty, 1986).

Unlike salmonids, fish employing an anguilliform swimming mode (e.g. lamprey) (Sfakiotakis et al., 1999) do not leap at migration obstacles and have limited burst swimming performance (Clough et al., 2004; Keefer et al., 2012; Russon et al., 2011). Although several lamprey species such as Pacific lamprey *Entosphenus tridentatus* can climb steep, smooth surfaces (Reinhardt et al., 2008; Kemp et al., 2009), most cannot and, like European river lamprey, use a combination of short burst-swimming followed by resting behaviour consisting of attachment to the substrate with their oral disc (Kemp et al., 2011; Russon et al., 2011; Moser et al., 2015), or undulation through shallow, slower flowing water. Foulds and Lucas (2013) showed pool and weir passes and steep Denil passes to be highly inefficient for European river lamprey passage.

In order to help restore free passage of fishes towards the community level, an increasingly inclusive approach is being adopted towards facilitating passage of a much wider range of species

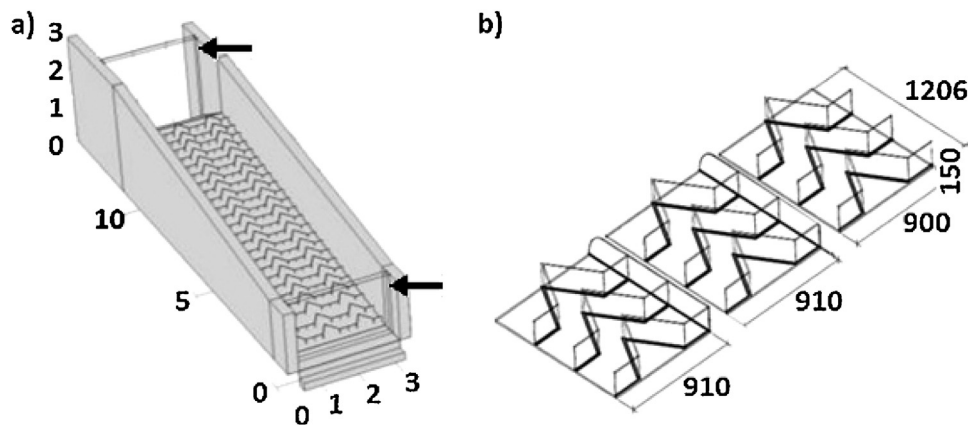


Fig. 2. (a) Schematic of Larinier super active baffle fish pass (grid-distances in m, PIT antenna arrays at downstream and upstream end of fish pass indicated by bold black arrow) with representation of baffles (detailed in b); (b) One of 24 baffle rows in total, dimensions in mm.

than had once been accommodated (Gough et al., 2012). This has taken the form of introducing nature-like fishways suited to a wide diversity of fish (and non-fish) taxa (Parasiewicz et al., 1998); modification of technical passes aiding a wide range of species and sizes (Mallen-Cooper and Stuart, 2007); and development of specific solutions for particular species and morphotypes, including thin-water-flow ramps for climbing lamprey species (Moser et al., 2011), and bristle and studded tile passes for elvers and yellow-stage freshwater eels (Solomon and Beach, 2004; Vowles et al., 2015).

Larinier super active baffle (SAB) fishways are relatively cheap retrofit fishways, suitable for low-head barriers (Larinier et al., 2002). They have become widespread in Europe and are the most commonly fitted technical pass in Britain. They are often intended to provide passage for a wide range of species (Armstrong et al., 2010), yet their suitability for non-salmonids, including lampreys, is poorly quantified. Since river lamprey are serpentine swimmers and positively thigmotactic, placement of studded tiles on the inner wall of single-flight fishways could allow for a continuous tile-route through the pass, with reduced flow velocity, low turbulence and increased availability of resting habitat. This study investigated the effectiveness of a Larinier SAB fish pass in facilitating upstream passage of adult river lamprey under varying flow conditions and water temperature, both before (2013–14, migration season 1, MS1) and after (2014–15, migration season 2, MS2) modifications with vertically mounted studded tiles on the inner wall of the fish pass.

2. Methods

2.1. Study site

The study was conducted at a 20 m wide Crump weir, at Buttercrambe (Lat: 54.018; Long: -0.8853; mean daily flow $17.1 \text{ m}^3 \text{ s}^{-1}$ (NERC, 2015)) on the River Derwent, Northeast England (Fig. 1). The Crump weir has a triangular profile (1:2 upstream and 1:5 downstream slopes), and was built in 1973 for monitoring river discharge, although ultrasonic gauging is now used instead. The weir is 40.2 river kilometres (rkm) from the Derwent confluence (Lucas et al., 2009), with a head loss of 1.31 m and discharge of $2.78 \text{ m}^3 \text{ s}^{-1}$ at Q_{95} (the flow equalled or exceeded for 95% of the time), annually (Environment Agency (EA), pers. comm.). The middle and lower Derwent comprises a series of low-gradient reaches (average gradient of 0.3 m km^{-1}) and is part of the Humber river system (mean daily flow $250 \text{ m}^3 \text{ s}^{-1}$). Draining the North Yorkshire Moors, the Derwent flows south and joins the Yorkshire River Ouse, which in turn combines with the River Trent to form the Humber estuary. This estuary provides suitable feeding habitat for parasitic

river lamprey growing to adulthood, and is a Natura 2000 Special Area of Conservation (SAC), for which river lamprey are a listed feature. Combined with spawning and recruitment areas in tributaries such as the Derwent, crucial habitats for river lamprey conservation occur within the Humber basin (Lucas et al., 2009), in which one of the most important UK river lamprey populations is sustained (Jang and Lucas, 2005).

The lower Derwent, where anadromous salmonid populations are slowly recovering after an absence lasting decades, but where cyprinid, percid and esocid fishes are abundant (Whitton and Lucas, 1997), is an area of importance for river lamprey conservation. Not only is it an SAC, it also forms one of the most impounded rivers within the Ouse catchment. Multiple anthropogenic structures (one tidal barrage and five low head (<3 m) obstructions, of which the barrage and two weirs are located downstream of Buttercrambe weir) have been constructed in the lower 60 rkm of the Derwent (Fig. 1). These impede free movement of multiple fish species, including river lamprey (Lucas et al., 2009). In May 2013 15% gradient Larinier SAB fish pass was opened at Buttercrambe weir, with the purpose of alleviating habitat fragmentation and restoring longitudinal connectivity for a variety of fish species, including river lamprey. Multiple sites with holding habitat (tree roots, boulders etc.) for lamprey are present immediately downstream of the weir. No artificial lighting in the vicinity of Buttercrambe weir nor the fish pass occurred during the study period.

2.2. Fish pass characteristics

The Larinier SAB fish pass, on the right side of Buttercrambe weir, is installed parallel to the main river flow. The Larinier pass (concrete, 11.2 m long, internal width 2.75 m) consists of 24 rows of super active stainless steel baffles (three per row, 12 mm thick, 150 mm high), equally spaced (0.40 m) and located across the pass's width (Fig. 2). These baffles are located on the downstream-facing ramp of the fish pass (9.8 m long and 1.47 m height difference, resulting in a fish pass gradient of 15%, or 8.5°). The invert of the pass is at 9.1 m above ordnance datum (mean sea level) and the upstream head on the pass (ha) is 0.32 m at Q_{95} . It has a head loss of 1.31 m at Q_{95} . For migratory salmonids and coarse fishes (cyprinids, percids and esocids targeted for recreational angling) exceeding 20 cm in length, a head difference of up to 1.8 m and 1.5 m in single-flight Larinier SAB fishways is advised, respectively (Armstrong et al., 2010). The lower operating depth limit for the fish pass is 0.17 m above the baffles, where a value of 0.10 m for coarse fish and 0.15–0.20 m for large migratory salmonids is advised (Larinier et al., 2002; Armstrong et al., 2010). The upper operating depth limit is dependent on the swimming capacity of each individual

Table 1
Details of PIT and acoustic tagged river lamprey per release date for each size of tag used (a, 23 mm PIT tag; b, 32 mm PIT tag; c, double-tagged with a 32 mm PIT tag and a 7.3 × 18 mm acoustic transmitter, respectively), for MS1 and MS2.

Date	Lamprey tagged (n)	Body length, mean ± SD (mm)	Detected at entrance (+exit)	Attraction efficiency (%)	Passage efficiency (%)	Median time to first detection (h)
31 October 13	a: 12, b: 55, c: 0	a: 352 ± 36, b: 351 ± 18, c: –	60(0)	89.5	0.0	502
06 November 13	a: 0, b: 74, c: 7	a: –, b: 348 ± 18, c: 381 ± 18	77(1)	95.0	1.3	358
14 November 13	a: 0, b: 68, c: 9	a: –, b: 359 ± 20, c: 394 ± 20	68(0)	88.3	0.0	167
21 November 13	a: 30, b: 27, c: 7	a: 357 ± 13, b: 357 ± 23, c: 389 ± 23	55(0)	85.9	0.0	3
26 November 13	a: 0, b: 32, c: 7	a: –, b: 364 ± 16, c: 364 ± 16	34(0)	87.2	0.0	3
06 December 13	a: 1, b: 20, c: 1	a: 341, b: 367 ± 24, c: 386	21(0)	95.4	0.0	125
Overall, MS1	a: 43, b: 276, c: 31	a: 350 ± 24, b: 358 ± 20, c: 389 ± 19	315(1)	90.1	0.3	25
28 October 14	b: 35	b: 354 ± 20	31 (9)	88.6	29.0	6
07 November 14	b: 14	b: 359 ± 21	8 (2)	57.1	25.0	6
21 November 14	b: 83	b: 362 ± 21	74 (1)	89.2	1.4	15
28 November 14	b: 51	b: 361 ± 21	44 (0)	86.3	0.0	5
04 December 14	b: 14	b: 364 ± 21	12 (0)	85.7	0.0	316
Overall, MS2	b: 197	b: 360 ± 21	169 (12)	85.8	7.1	6

fish species. The upstream-facing ramp, where baffles are absent, is 1.4 m long and has a constructed height difference of 0.47 m at a 33% gradient. There is a 0.35 m vertical step between the downstream end of the fish pass and the river bed. The Larinier pass inundates fully at $<Q_3$ (J. Tummers, pers. obs.). The pass's position on the right hand bank of the river is immediately upstream of a left-bend of the river, so that it is upstream of the dominant flow on the outside of the bend, thereby potentially facilitating attraction to the fishway entrance for fish moving upstream. An elver pass (bristle substrate within conduit) is located on the left bank, designed for European eel *Anguilla anguilla* elvers and small yellow eel.

In summer 2014, modifications to the fish pass were made with the aim of enhancing passage efficiency for anguilliform fish, including river lamprey. Modified 'eel tiles' (Berry and Escott Engineering, UK) were vertically mounted on the inside right-hand fish pass wall (Fig. S1; engineering design images available at <http://berryescott.co.uk/Lamprey-Tiles>). These consisted of 2 cm thick polypropylene boards (1.02 m long, 0.50 m wide) each covered with 72 studs, projecting towards the fishway wall, with the boards mounted vertically, adjacent to the wall. Studs were blunt-ended cones, 50 mm high and 30 mm base diameter, separated by 55 mm along rows and 88 mm at diagonals of the stud bases. Studded tiles were housed within wall-mounted aluminium brackets to provide lift-out boards for cleaning of debris. Starting 0.3 m upstream of the fish pass entrance (due to the presence of a passive integrated transponder (PIT) antenna, see below), the tiles were placed continuously to the fish pass exit region, 0.3 m beyond the upstream-most PIT antenna. This allowed for a partially separated passage route along the right wall edge, with increased resting habitat and reduced flow velocities housed within the Larinier fish pass. Since the Larinier baffles were designed to fit the breadth of the pass and were not modified, the studded tiles, which were open at the bottom, made contact with the baffles' upper surfaces, rather than the fishway's concrete base. While the studded tiles did not extend to the bed, the arrangement allowed lamprey entering the main pass to access the studded media at any point along the pass.

Hydrodynamic conditions of the Larinier SAB fish pass were measured both within, and at the downstream entrance of, the fish pass at 0.23 m river stage, weir crest 9.65 m above UK mean sea level, 0.40 m head in pass (25 September 2013, Q_{85} , no studded tiles in place) (Fig. 3). An electromagnetic water velocity meter (Valeport model 801) was used to take an array of point-measurements of mean flow velocity (\pm SD, in m s^{-1}), each over a 20 s period. Every 0.3 m along the channel, at a distance of 0.2 m and 0.4 m from the bed (0.05 m and 0.25 m above the top of baffle surface, respectively), seven measurements (equally spaced, 0.4 m intervals) were taken across the width of the fish pass (238 measurements at

each depth, for a grand total of 476 measurements), corresponding to the number of relatively slow-flowing lanes ($n=4$) and relatively fast-flowing lanes ($n=3$), the latter occurring in the V-apex regions of the baffles. Based on flow velocity measurements, discharge through the fish pass was calculated by multiplying velocity with cross sectional area of flow. The proportion of total river discharge entering the Larinier fish pass was estimated at 15.8% (25 September 2013, Q_{85}).

2.3. Lamprey capture and tagging

Because catch per unit effort of river lamprey in the Derwent is low (Jang and Lucas, 2005), migrating lamprey for the study were captured from the Yorkshire Ouse in two-funnel eel pots (Masters et al., 2006) and taken to Buttercrambe for tagging and release. Lucas et al. (2009) demonstrated no difference in migration behaviour of Derwent-caught and Ouse-caught lamprey released in the Derwent. Natal homing behaviour is absent for the strongly positively rheotactic river lamprey (Tuunainen et al., 1980) and river lamprey in tributaries of the Ouse are the same genetic population (Bracken et al., 2015).

Lamprey for tagging were anaesthetised (stage III, surgical) using a buffered 0.1 g L^{-1} solution of MS-222. Total body length in mm was measured and lamprey were subsequently tagged by implanting a 32 mm × 3.65 mm or a 23 mm × 3.65 mm PIT tag (HDX, Texas Instruments model RI-TRP-RRHP, 134.2 kHz, weight 0.8 g and 0.6 g in air, respectively) into the body cavity via a mid-ventral incision under UK Home Office Licence following the Animal Scientific Procedures Act 1986. A single suture (coated Vicryl, 4/0) was used to close the incision. In MS1 a sample of the 32 mm PIT tagged fish were also tagged with a coded 69 KHz acoustic transmitter (Model LP-7.3, 18 mm long × 7.3 mm diameter, 1.9 g in air, 30–60 s code interval nominal repeat, Thelma Biotel AS, Trondheim, Norway). After acoustic tagging, the incision was closed with three separate sutures. Table 1 shows numbers and body lengths of river lamprey tagged solely with PIT tags (23 mm and 32 mm) and double-tagged with a 32 mm PIT tag and acoustic tag, for the two study seasons. In total, 350 lamprey were PIT tagged in MS1, of which 31 were double-tagged with an acoustic tag, and 197 individuals were PIT tagged with 32 mm tags solely in MS2. Fish were allowed to fully recover (ca. 45 min) in aerated water before release 0.16 km (PIT tagged lamprey) or 0.62 km (acoustic + PIT tagged lamprey) downstream of the weir. Acoustic tagged fish were released further downstream to enable upstream-moving lamprey to be recorded as they approached the weir.

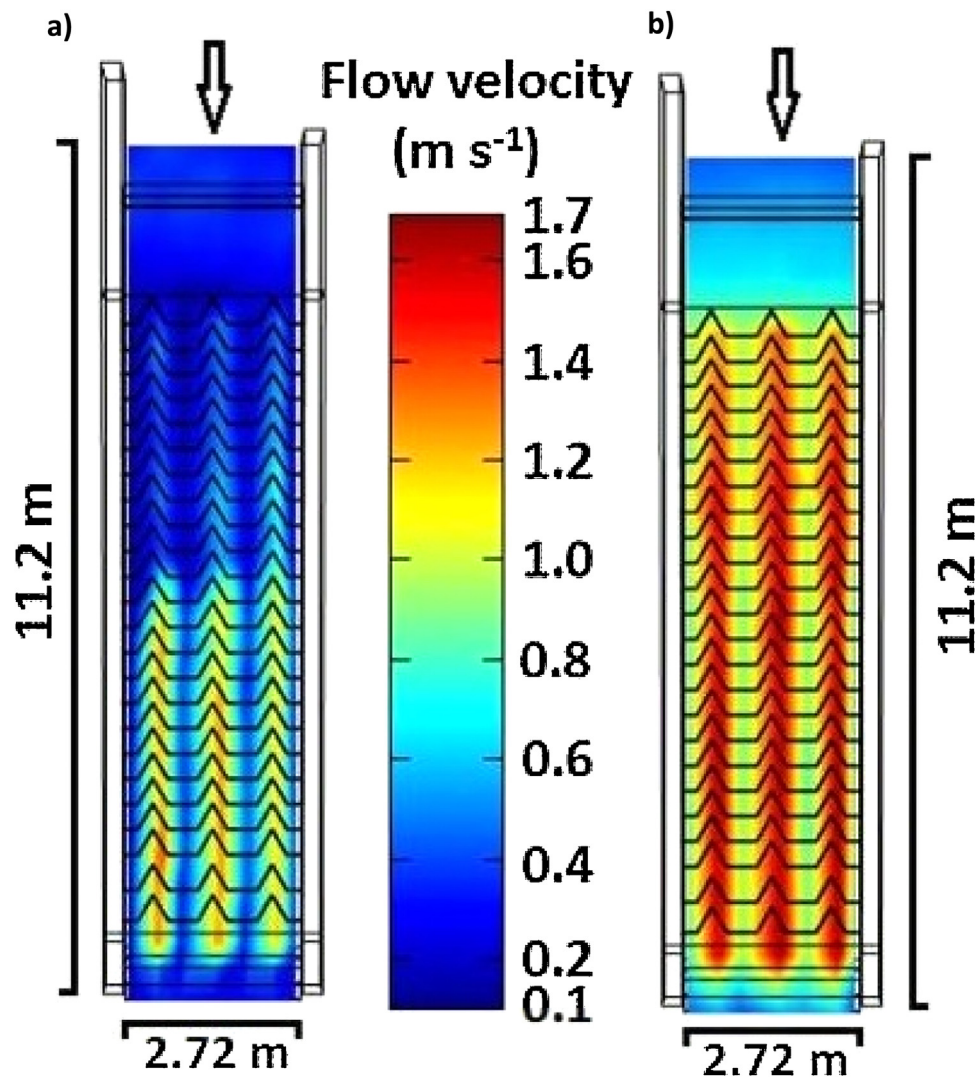


Fig. 3. Flow velocity measurements (m s^{-1}) taken at 0.20 m from bed (0.05 m from top of baffles (a), left) and 0.40 m from bed (0.25 m above top of baffles (b), right) within the Larinier fish pass. Stage height measurement on the day of measurement was 0.23 m (Q_{85}) and depth within the fish pass was 0.50–0.55 m.

2.4. Telemetry

A pass-through synchronised Master-Slave half-duplex (HDX) PIT detection system (Wyre Microdesign, UK) based upon the design of [Castro-Santos et al. \(1996\)](#) was installed in the Larinier pass. Antennas made of 6 mm diameter, 771 strand, oxygen-free copper insulated wire were placed at the downstream and upstream ends of the fish pass (2.75 m wide \times 1.62 m high for downstream antenna; 2.75 m wide, 2.3 m high for upstream antenna), ca. 0.5 m from upstream exit and 0.3 m from downstream entrance. Each antenna terminated in a tuning box at the top of a pole positioned vertically on the right side wall of the fish pass. A data and power cable connected the tuning box to the readers and logger. Power was provided by a 12 V leisure battery, trickle charged by a linear mode battery charger from a 240 V AC mains supply.

The Larinier pass antennas were tuned to ensure detection of a 32 mm long PIT tag at any point and orientation within the loop, with a typical perpendicular range from the loop axis of 0.3 m. The antennas were also tested with 23 mm PIT tags and while complete coverage was achieved at both antennas in May 2013 (within a month of antenna placement) by October 2013, a detection hole of ca. 0.5 \times 0.5 m was evident in the centre of the upstream antenna for 23 mm tags. For 32 mm tags, no holes in the detection field

were found, despite repeated, intensive tests over the whole study period, nor for 23 mm tags at the downstream antenna. Therefore, 32 mm tags were used to tag lamprey. A subset of lamprey were tagged with 23 mm tags used to determine any possible impact of the larger tag. Synchronised HDX (Texas Instruments) readers were used to interrogate the paired antennas simultaneously (13 times per second), so as to ensure no signal interference. As well as regular manual percentage detection efficiency tests (>99% on all occasions), timed auto-emitter check tags (Oregon RFID, USA) were used to monitor operational efficiency of the PIT equipment.

Logging equipment ran continuously (>99.9% of time) from 31 October 2013 to 26 February 2014 (MS1) and from 28 October 2014 to 26 February 2015 (MS2). This is a period that incorporates over 95% of lamprey upstream migration activity in the Derwent ([Lucas et al., 2009](#); [Foulds and Lucas, 2013](#)). Upon detection, the tag's unique code, date and time were stored. This allowed for determination of: a) the proportion of lamprey released downstream recorded at the fishway entrance (attraction efficiency); b) the proportion of lamprey successfully ascending the fish pass, after having located the entrance (passage efficiency; ([Aarestrup et al., 2003](#); [Cooke and Hinch, 2013](#))) and c) patterns of visitation to the Larinier fish pass. Attempt frequencies by individual lamprey were extracted employing a 1 h minimum interval filter between repeat

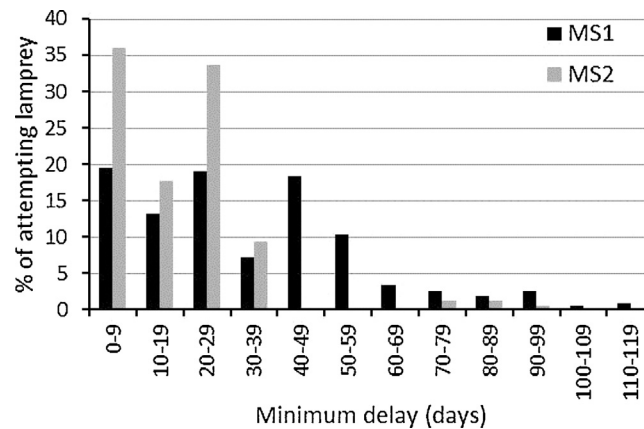


Fig. 4. Minimum delay periods for individual lamprey migration (days) at Buttercrambe as a percentage of those that entered the fish pass (total of $n = 315$ and $n = 169$ for MS1 and MS2, respectively). Duration calculated from PIT records from release day until last detection at downstream entrance of fish pass.

detections, assumed to reflect more extensive searching behaviour for alternative routes and/or extended periods in the fish pass. Cooke and Hinch (2013) distinguish attraction (detection in the pass outflow vicinity, *ca.* <3 m below the fishway) from entrance (detection in the lowest part of fishway) behaviours and define entrance efficiency as the proportion of fish detected in the pass outflow vicinity which then enter the pass. Perhaps unhelpfully, detection of fish entering the pass without prior instrumentation and associated detection in the fishway outflow has no definition in Cooke and Hinch's (2013) scheme. In our experiments we consider the proportion of released lamprey that visited the fishway entrance as an appropriate measure of attraction efficiency. Piscivores (birds, mammals and fish) occur near Buttercrambe weir (J. Tummers, pers. obs.; Whitton and Lucas, 1997) and may contribute to natural mortality of tagged lamprey, so our attraction efficiency measurement is a minimum estimate. Passage efficiency in the Larinier fish pass was calculated only for 32 mm PIT tagged lamprey due to the central detection 'hole' in the upstream antenna for 23 mm PIT tags.

Since some lamprey can pass Derwent weirs directly by the main river channel (Lucas et al., 2009), and because PIT detection antennas could not cover the whole river width and depth, coded 69 KHz acoustic transmitters and receivers (Vemco VR2, Halifax, Canada) were used in MS1 to evaluate passage by this route. Three omnidirectional receiver-loggers were placed at varying distances (~45–380 m) upstream of the weir in areas of non-turbulent (low-noise) water, while five were placed 160–4600 m downstream of Buttercrambe weir. All eight receivers were operational from 26 October 2013 to 26 February 2014. Detection radius (45–75 m) varied by receiver. No test tags placed at any location downstream of the weir could be detected by receivers upstream of the weir. First records of acoustic tagged fish at the first receiver downstream of the weir were classified as fish approaching (and attempting to pass) the weir, while the same fish could be detected at the fish pass entrances, by virtue of their PIT tags.

For MS2, extra PIT antennas were placed in the Larinier pass to assess the efficacy of the fish pass after addition of studded tiles. In addition to the PIT antennas fixed on the downstream entrance and upstream exit from MS1, a low-range PIT antenna (3 mm diameter, multistrand insulated copper wire) was formed on the inside of a tile 1 m upstream of the fish pass entrance, and within a tile placed 1 m below the upstream exit. Tiles closer to the fishway ends were present, but not chosen for antenna placement to ensure unique detection fields of each antenna and avoid electrical noise transfer. Antennas detection characteristics were tested rigorously, particularly to ensure that tile antenna detections were for tags within (not outside) the tile. The four PIT antennas ran continuously (>99.9% of

the time) in MS2, from 28 October 2014 to 26 February 2015. All tiles were visually inspected and cleaned approximately every 2 weeks during MS2.

2.5. Environmental conditions and statistical analysis

Ultrasonically gauged stage and discharge at Buttercrambe weir were obtained from the EA. Flows were related to the percentage of annual exceedance (Q_x) by using an annual flow duration curve (<http://www.ceh.ac.uk/data/nrfa/data/time-series.html?27041>). Water temperature was logged at 1 h intervals (Tinytag, TG-4100), 150 m downstream of Buttercrambe weir.

Cosmos Multiphysics 5.0 was used to create fish pass velocity profiles from empirical data. Differences between number of detections and attempts by lamprey at both fish passes (between MS1 and MS2: Mann–Whitney U test; between release dates within MS1 or MS2: Kruskal Wallis test) and effects of environmental factors (General linear model (GLM)) were analysed for significance using SPSS 22. R 3.2.0. was used to create plots of diel activity and to relate environmental factors to lamprey attempts made at the fish pass. Data were examined for normality and homogeneity of variance before determining suitability of parametric or non-parametric statistical approaches. Benjamini–Hochberg corrections were made to multiple-comparisons of non-parametric data.

3. Results

3.1. Fish pass efficiency and time taken to locate the pass entrance

Although 315 out of 350 lamprey released below Buttercrambe weir were detected at the entrance of the Larinier fish pass in MS1 (attraction efficiency, 90.1%), only one (0.3%) successfully ascended it during the period 31 October 2013 to 26 February 2014 (119 days) (Table 1). There was no significant effect of tag size and double-tagging treatment on the numbers of lamprey detected at the Larinier pass (χ^2 test; $df = 2$, $\chi^2 = 0.9994$, $P = 0.603$). When comparing time to first detection for individuals tagged with 23 mm or 32 mm PIT tags on paired release days ($n = 2$), in the first release 32 mm tagged lamprey were detected in the fishway sooner than 23 mm tagged lamprey (Mann–Whitney; $U = 169.5$, $Z = -2.213$, $P = 0.027$; 23 mm tags, $n = 12$; 32 mm tags, $n = 55$), a counterintuitive outcome, suggesting no tag burden impact. No significant difference occurred for lamprey released on 21 November 2013 (Mann–Whitney; $U = 279.0$, $Z = -0.875$, $P = 0.381$; 23 mm tags, $n = 30$; 32 mm tags, $n = 27$).

During MS2, with lamprey tiles installed on the inner side of the right wall of the fish pass, 169 out of 197 released lamprey

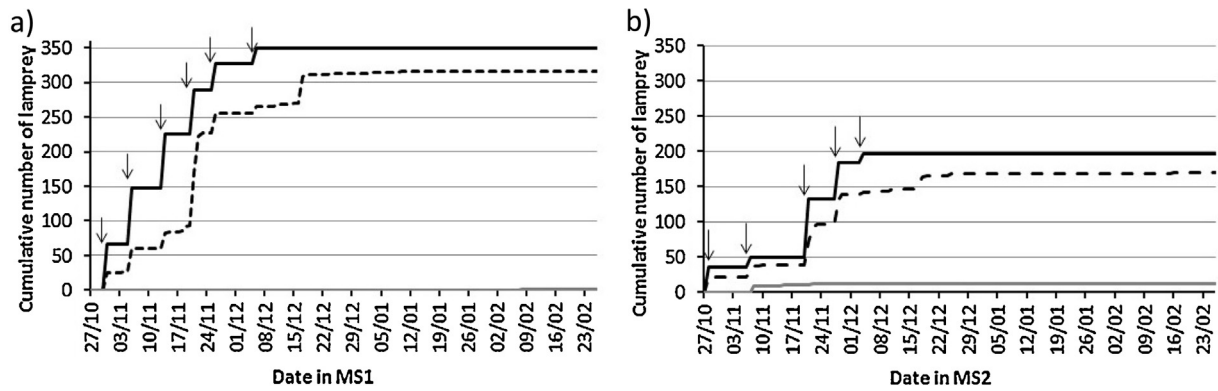


Fig. 5. (a) Cumulative number of lamprey at liberty (solid black), number of lamprey detected at the fish pass entrance (dashed) and number of lamprey successfully ascending the fish pass (grey) in MS1 and (b) in MS2. Note that during MS1, one lamprey successfully ascended the SAB fish pass on 08/02/2014. Arrows indicate release dates.

entered the fishway (85.8% attraction efficiency). Twelve lamprey (7.1% passage efficiency) were successful in ascending the fish pass (Table 1) all of which used the tile-route. On 18 December 2014, two of the tiles were found to be missing (both located directly upstream of the lower instrumented tile). These were not replaced as the brackets were bent and would have required fishway closure for repair. As a result, the tile-route was subsequently discontinuous; during this period no tagged lamprey detections were made at the upstream tile PIT antenna nor at the upstream exit PIT antenna, but the detection rate at the downstream tile PIT antenna fell to 23.4% (15/64) of the rate prior to 18 December 2014, while the detection rate of lampreys entering the pass fell to 49.0% (74/151) of the rate prior to 18 December 2014.

Of the 315 lamprey which entered the SAB fish pass in MS1, 158 (50.2%) were detected at the downstream antenna within 24 h of release. In MS2, 105 out of 169 (62.1%) of lamprey entered the pass within the same period. There was no significant difference in time to locate the fish pass between the two migrating seasons (MS1; median time = 25 h [range: 1–1386 h]; MS2; median time = 6 h [range: 2–2074 h], Table 1; Mann–Whitney; $U = 24201.0$, $Z = -1.650$, $P = 0.099$). Excluding lamprey that never located the fish pass during the study period, there was a significant difference in time taken to locate the fishway across the six release dates in MS1 (Kruskal Wallis; $H = 26.71$, $df = 5$, $P < 0.001$). Using post-hoc pairwise analyses (Mann–Whitney U corrected with Benjamini–Hochberg false discovery rate), significant pairwise differences were found in MS1 between release dates 31 October–06 November, 31 October–21 November, 31 October–26 November, 06 November–21 November, 14 November–21 November, 21 November–06 December and 26 November–06 December. For MS2, a significant difference was found for time taken to locate the fish pass across five release dates (Kruskal Wallis; $H = 11.40$, $df = 4$, $P = 0.022$), but after post hoc pairwise comparisons corrected for false discovery rate, no significant difference was apparent.

3.2. Fish pass ascent attempts

The 315 river lamprey that located the fish pass in MS1 had a mean attempt frequency at the SAB pass of 11.4 (range: 1–177), while the 169 individuals released during the 2014–2015 migrating season attempted the fish pass 7.3 times on average (range: 1–28) over the whole study period. Many lamprey were in the vicinity of the fishway for a prolonged period in both study seasons (Fig. 4). While 62 individuals (19.7%) were only detected at the SAB entrance within 10 days of release, a substantial proportion (33, or 10.4%) were present downstream of the weir even from 50–59 days after release in MS1. After modification of the fish pass, 61 (36.1%) were detected within 10 days after release, while 16 lamprey (9%)

were in the vicinity of the pass 30–39 days following release (Fig. 4). Individual lamprey were delayed for a mean minimum of 32.8 and 16.5 days, for the first and second migrating season, respectively.

Temporal patterns of river lamprey visits to the SAB pass were affected by day of release as well as river flow (Fig. 5). Using 16 January 2014 and 2015 as cut-off dates, after which negligible numbers of lamprey were attempting to pass the SAB fish pass, but when river discharge was markedly higher relative to the preceding part of the study period for MS1 (Fig. 6), the number of attempts made at the fishway was positively but weakly affected by river flow in MS1 (GLM: $F_{1,70} = 4.964$, $P = 0.029$, $R^2 = 0.066$). There was no relationship between water temperature (mean \pm SD during MS1: $5.59 \pm 0.93^\circ\text{C}$) and number of attempts in MS1 (GLM: $F_{1,70} = 1.893$, $P = 0.173$, $R^2 = 0.026$). Combining flow and water temperature factors gave a positive relationship with attempt frequency (GLM: $F_{2,69} = 3.719$, $P = 0.029$, $R^2 = 0.097$). By contrast, in MS2 (water temperature mean \pm SD: $5.04 \pm 1.90^\circ\text{C}$), a dominant flow effect was found (GLM: flow $F_{1,74} = 15.086$, $P < 0.001$, $R^2 = 0.169$); water temperature ($F_{1,74} = 1.778$, $P = 0.187$, $R^2 = 0.023$); flow plus water temperature ($F_{2,73} = 7.538$, $P < 0.001$, $R^2 = 0.171$). The highest number of individuals detected at the fish pass in a day was, for MS1, on 17 December 2013 (182 lamprey, 52% of lamprey released at the time, mean daily flow of $22.7 \text{ m}^3 \text{ s}^{-1}$ (Q_{24}), mean daily water temperature of 7.18°C , Fig. 6). For MS2, this was on 18 December 2014 (64 lamprey, 32.5% of lamprey at liberty at the time, mean daily flow of $22.3 \text{ m}^3 \text{ s}^{-1}$ (Q_{25}), mean daily water temperature of 6.28°C , Fig. 6).

Not including release dates, in MS1 and MS2, 58.4% and 59.1% of attempts respectively (with a minimum interval of 1 h) were made after evening civil twilight and before morning civil twilight times for the locality. Lamprey attempts were made particularly during late afternoon and early evening, when transition from light to dark conditions is (close to be) completed during late autumn and winter, for both seasons (Fig. S2).

3.3. Acoustic telemetry of lamprey approaching the weir

In MS1 all 31 double-tagged (PIT and acoustic) river lamprey were logged at the first acoustic receiver upstream of the release site. Twenty nine (93.5%) lamprey visited the weir, and 20 (64.5% of total) did so within 3 h of release. Based upon time of first and last detection at successive receivers, these had a net speed over ground of 0.34 body lengths per second which, combined with the average water velocity in the reach under these conditions (0.37 m s^{-1}), gave an average sustained swimming speed of 1.30 body lengths per second during the upstream movement. Although 93.5% of acoustic-tagged lamprey visited the weir vicinity, fewer (23, 74.2%) visited the SAB pass and none ascended it.

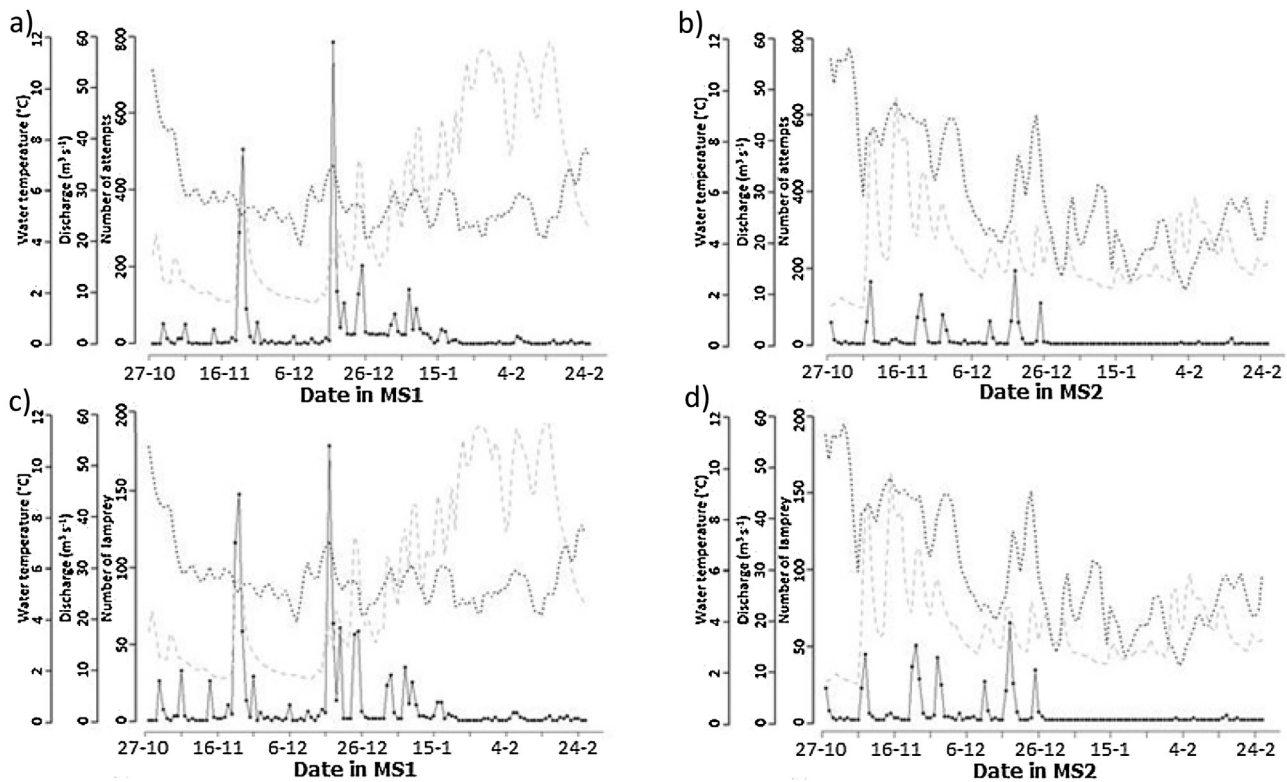


Fig. 6. (a), (b); Number of lamprey passage attempts, using a ≥ 1 h interval filter between successive attempts for the same individual, relative to temperature and river discharge per date in MS1 and in MS2, respectively. (c), (d); Number of unique lamprey per day detected at downstream entrance of fish pass relative to temperature and river discharge per date in MS1 and in MS2, respectively. Bold black: number of attempts/lamprey; dotted black: temperature ($^{\circ}\text{C}$); dashed grey: river discharge ($\text{m}^3 \text{s}^{-1}$).

Four of 29 (13.8%) acoustic tagged lamprey that visited the weir vicinity were detected at acoustic receivers upstream of the weir; none subsequently returned downstream. Water levels in MS1 (31/10/2013–26/02/2014) were not high enough to overtop banks at the weir and create extra spillways around the weir (occurs at $<Q_3$). These four lamprey are therefore interpreted to have traversed the main channel weir. The four successful lamprey passed at flows of $13.8 \text{ m}^3 \text{s}^{-1}$ (Q_{44}), $18.8 \text{ m}^3 \text{s}^{-1}$ (Q_{26}), $34.3 \text{ m}^3 \text{s}^{-1}$ (Q_{10}), during which tailwater levels were elevated, but the weir was not fully drowned, and $43.9 \text{ m}^3 \text{s}^{-1}$ (Q_5), at which the weir was nearly drowned (J. Tummers, pers. obs.).

4. Discussion

European river lamprey did not effectively use the Larinier SAB fishway, a design widely used in Europe at low-head structures, often with the aim of passing a wide range of fish species (Armstrong et al., 2010; Larinier et al., 2002). The unmodified SAB pass exhibited similar attractiveness and low passage efficiency to that found by Foulds and Lucas (2013) for river lamprey at pool and weir and Denil passes on the same river, using similar methods. A forty times higher passage rate was observed for double-tagged (acoustic and PIT) lampreys (albeit small sample size) at the weir itself than through the SAB fishway, even though the weir was never fully drowned. Attraction efficiency was high in both MS1 and MS2 (90.1% and 85.8%, respectively) and numerous ascent attempts were made at the fishway (mean attempt frequency per individual lamprey of 11.4 and 7.3 in MS1 and MS2) under a broad range of flow conditions. Reported attraction efficiency in this study is a minimum, since it is possible that some PIT tagged fish lingering at the downstream antenna blocked detection of others (Cooke et al., 2012), and also because some tagged lamprey are likely to have been predated before visiting the fish pass. The majority of lam-

prey had located the fish pass within 24 h of release (50.2% in MS1, 62.1% in MS2), indicating strong motivation to pass. This suggests that some element of the unmodified SAB greatly inhibited lamprey ascent, but not their attraction to the pass.

The most obvious candidate factor inhibiting lamprey ascent in the unmodified SAB would be excessive flow velocity, exceeding the swimming capabilities of river lamprey. Modelled average velocity (Larinier et al., 2002; Armstrong et al., 2010) above the baffles for the unmodified SAB pass varied from 1.3 m s^{-1} at Q_{99} to 1.8 m s^{-1} at Q_{30} and in excess of 2 m s^{-1} at flows greater than Q_{20} . Observed burst swimming performance of river lamprey is known to be at least 2.12 m s^{-1} at 12.6°C for an experimental undershot weir (Russon and Kemp, 2011), although 1.5 m s^{-1} may be a more typical value (Kemp et al., 2011). In Finnish studies this species (25–30 cm long, smaller than our 35–40 cm Humber river lamprey) has been shown to successfully ascend bristle-lined vertical slot fish passes in Finland with maximum flow velocities of 1.4 m s^{-1} (Laine et al., 1998). River lamprey are thigmotactic and bed- and edge-orientated during passage of obstructions (Kemp et al., 2011), and like other lamprey species are effective at utilising slower areas (Keefer et al., 2011; Moser et al., 2015), including boundary layer regions (M. Lucas, pers. obs.). Our empirical measurements of flow velocity at Q_{85} demonstrated three- to four-fold regional variations in water velocity horizontally across the fish pass (Fig. 3). Highest values of flow velocity occurred at the V-apex regions, and an approximately two-fold difference in water velocity was measured between depths of 5 cm and 25 cm above the baffles (Fig. 3). Therefore, at higher river flows with a modelled above-baffle velocity estimate of 1.8 m s^{-1} , one would still expect regional velocities to be well within limits exploitable by river lamprey. Undoubtedly the distance of the high-velocity zone to be traversed in the Buttercrambe SAB fishway (9.8 m to crest) is more than the values of 1–2 m in laboratory swimming performance studies (Kemp

et al., 2011; Russon and Kemp 2011). However, like other lamprey species, river lamprey commonly use a “burst-attach-rest” mode of locomotion, enabling partial recovery between burst swimming bouts as observed for sea lamprey (Quintella et al., 2004), and this might be expected to facilitate SAB passage by river lamprey.

A more likely reason for river lamprey failing to ascend the unmodified SAB fishway relates to the bed-mounted baffle plates. Slowing of average water velocity in SAB passes is achieved by the baffles creating helical currents that dissipate energy (Larinier et al., 2002). Inevitably this generates a large amount of turbulence above and between the baffles. Keefer et al. (2010) demonstrated Pacific lamprey to have major difficulties in the transition from stationary attachment to resuming upstream movement under turbulent conditions at bulkhead challenges. The majority of lamprey failed in re-attaching and consequently were swept downstream. Identical difficulties have been observed for river lamprey within a Denil baffle fish pass (W. Foulds, pers. comm.). Vowles (2012) found no effect of local turbulence on passage success of river lamprey in laboratory studies, although his experimental design examined simplified localised turbulence generated by a single cylinder, unlike in a baffle fishway. For river lamprey, with an anguilliform body morphology lacking paired fins that facilitate stability (Liao, 2007), the cumulative effect of attempting to traverse the 24 rows of baffles present in the Larinier fish pass evaluated in our study is therefore likely to be considerable. Such conditions may strongly inhibit continued upstream progression (performance) or might stimulate lamprey to give up, move downstream and seek an alternative route (volitional behaviour). Furthermore, bed-mounted baffles might inhibit the natural thigmotactic, bed-orientated upstream movement behaviour of lampreys and cause rejection of this environment. In this study, baffle units were approximately 40 cm apart (slightly greater than an average river lamprey length) and 15 cm high, common dimensions in SAB passes. A typical lamprey passing a baffle and moving to the bed to attach using its oral disc, part-way between adjacent baffles, could therefore trail its tail over the downstream baffle or be bent within the baffle unit. In either case they are subject to helical turbulent flow, which potentially causes rejection of the local environment and downstream movement. Observation *in situ* at the SAB fishway was not possible because of low visibility (Secchi depth ca. 0.05–0.50 m during the study) and entrained air. Determination of which of these factors is responsible for failure of lamprey to ascend the unmodified SAB requires experimental flume studies. Determining the reason why river lamprey reject SAB baffles has wider relevance as it might apply to other lamprey species including landlocked sea lamprey in the Laurentian Great Lakes region. In that region, provision of selective barriers that prevent sea lamprey passage, but allow passage of other migrating fish is a key objective (Pratt et al., 2009).

Understanding how river lamprey directly passed the Crump weir in this study deserves consideration, since typical flow velocity would be expected to be in the region of 3 m s^{-1} for this type of structure, beyond the burst-swimming performance of river lamprey (Russon and Kemp, 2011). River lamprey are known to pass drowned weirs (Lucas et al., 2009), but for only one of four acoustic tagged lamprey passing the weir in this study was the weir almost drowned, not in the other three. No alternative routes other than the weir and fishway were available. Since otter *Lutra lutra*, grey heron *Ardea cinerea* and goosander *Mergus merganser* have been observed at the site it is possible, but very unlikely, that one or more acoustic tags could have been ingested by a terrestrial predator which then moved upstream. Otter do not ingest whole lamprey prey (M. Lucas, pers. obs.), and several tags from our study were found on the left bank at an otter feeding site, 10 m downstream of the weir (J. Tummers, pers. obs.). Grey heron and goosander have been observed very infrequently in the deep water immediately upstream of the weir, compared to the shallower area downstream

(J. Tummers, M. Lucas, pers. obs.). In an experimental flume, river lamprey failed to pass a Crump weir with a maximum mean velocity at the weir face of 2.30 m s^{-1} (Russon et al., 2011), although those experiments employed much lower water depths at the weir face than occurred at Buttercrambe. Therefore, it is likely that lamprey negotiated the weir by searching for lower-velocity edge areas or crevices before passing it (see also Kemp et al., 2011). Since the weir is in a good state of repair, the most likely route was at the junction between the wing-wall and weir-face, since lamprey have been observed accumulating immediately downstream of that locality during lower-flow, clear-water conditions (M. Lucas, pers. obs.).

For Pacific lamprey, it has been shown that high energetic costs during migration (e.g. frequent attempts at a fish pass) may impact the individual's fitness, likely compromising both behavioural and physiological processes crucial for sexual maturation and successful spawning (Mesa et al., 2003). This is especially problematic for lampreys, including river lamprey, as their gut degenerates and feeding (i.e. energy intake) ceases when adult lamprey enter freshwater for their upstream migration (Lucas and Baras, 2001; Moser et al., 2015). They have a fixed energy reserve and are semelparous; individuals unable to locate suitable spawning grounds have zero fitness. Foulds and Lucas (2013) also recorded high rates of attempts by river lamprey to ascend fish passes. While adoption of “burst-attach-rest” locomotion might delay exhaustion during ascent attempts, full recovery by staying attached to substrate for a prolonged time is unlikely. In electromyogram telemetered sea lamprey negotiating rock weirs, an increasing onset of fatigue was recorded after each burst movement, likely resulting from resuming burst swimming without fully recovering physiologically from preceding efforts (Quintella et al., 2004).

Low efficacy of the SAB fishway on river lamprey is also reflected in migration delay, shown in this study to be considerable for both spawning seasons (mean minimum delay days for individual lamprey was 32.8 and 16.5 days for MS1 and MS2). These migration delays below the weir are underestimates, as a large proportion of lamprey not recorded as passing upstream may be regarded as being delayed for the entire study period rather than the period between first and last detection, as used in this study. A delay in migration can increase physiological stress, susceptibility to disease (Loge et al., 2005) and risk of predation (Rieman et al., 1991; Peake et al., 1997). Predation of lamprey due to otter occurred during this study, as lamprey mortalities together with loose PIT tags, an acoustic transmitter, and otter spraints were located below Buttercrambe weir. Furthermore, piscivorous birds grey heron and goosander have been observed catching river lamprey (J. Tummers, M. Lucas, pers. obs.), and northern pike, known to predate river lamprey, are abundant at the weirpool (J. Tummers, unpublished data). Lucas and Baras (2001) argue that to achieve effective reconnection of fragmented river sections for diadromous species requires a minimum passage efficacy of 90% per site, because of cumulative losses at successive obstacles. Access to spawning habitat for river lamprey on the lower Derwent is poor; Lucas et al. (2009) reported 98% of lamprey spawning habitat on the lower Derwent occurred upstream of Buttercrambe weir, where on average only 1.8% of lamprey spawners occurred. Based on our results, river lamprey in the lower Derwent are severely affected in their spawning migration, and consequently probably also in their fitness.

Like other lampreys, adult European river lamprey probably use a combination of cues to guide their spawning migration (Moser et al., 2015). Adult river lamprey are sensitive to putative pheromones released by freshwater larval river lamprey (Gaudron and Lucas, 2006), and this likely plays a role in their upstream migration in a manner similar for sea lamprey (Wagner et al., 2009; Vrieze et al., 2010, 2011). It is also well documented that river lamprey exhibit positive rheotaxis, moving upstream against the river current, whereby migratory activity is positively corre-

lated with river discharge (Masters et al., 2006; Foulds and Lucas, 2013; Aronsuu et al., 2015). In our study, the frequency of passage attempts and number of lamprey recorded at the SAB pass was positively correlated with river flow, but only weakly in MS1 when early autumn flows were unusually low, and strong attraction to the fishway occurred even during low flows. During high flow events, peaks in detections at the fish pass were logged in both years. River lamprey are regarded as negatively phototactic during their spawning migration (Sjöberg, 1980), but this study and that of Foulds and Lucas (2013) suggest a much wider range of activity than typified by the nocturnal behaviour of lampreys. River lamprey swim close to the river bed, where flow velocities are lower (Lucas et al., 2009; Kemp et al., 2011). As water levels rise, light penetration to the river bed is decreased because of higher turbidity and increased water depth (Aronsuu et al., 2015), and risk of predation is likely to be lower, which may partly explain increased migratory activity, including by day, during elevated water levels.

Fish swimming capacity typically decreases with lower water temperature below the thermal optimum (Wardle, 1980; Videler, 1993). Higher water temperatures, below the thermal optimum, enhance recovery from exhaustive exercise (Wilkie et al., 1997) and increase the potential for aerobic activity used for sustained swimming (Goolish, 1989; Videler, 1993). In our study, no effect of water temperature alone (mean \pm SD during MS1 5.59 ± 0.93 °C; MS2 5.04 ± 1.90 °C) was found on the rate of passage attempts. Aronsuu et al. (2015) identified Finnish autumn-migrating river lamprey to be thermotactic, in that increased activity was triggered by a quick, relatively large decrease in water temperature, but as temperatures fell close to freezing they became stationary in winter holding-habitat. We found that lamprey were inactive in attempting the fish pass during relatively low water temperatures (ca. 2 °C) at the end of MS2, when river lamprey upstream migration activity in the UK has ceased anyway. Other studies have shown water temperature to have important implications for fish passage; adult Atlantic salmon (*Salmo salar*) had major difficulty ascending a fish ladder in a Scottish river when water temperature was below 8.5 °C (Gowans et al., 1999), and Rustadbakken et al. (2004) found that a weir in Norway formed an obstruction to upstream migrating adult brown trout (*Salmo trutta*) at ca. 6 °C, but at ca. 8 °C free passage was recorded.

Modification of the SAB fishway with wall-mounted tiles increased passage efficiency by over 20-fold, from 0.3% to 7.1%. This is promising, but it is still well below the 90% efficiency target that Lucas & Baras (2001) suggest is appropriate. Reduced local flow velocity in combination with increased availability of resting habitat within the tiles may have facilitated increased passage. Two of the vertically aligned lamprey tiles were found to be missing on 18 December 2014 (both located just above the downstream instrumented tile), likely due to debris damaging the brackets in which the tiles were fitted. Passage efficiency for the whole study period in MS2 was 12/169 (7.1%), and before tiles were missing it was 12/151 (7.9%). This date was 52 days into the 2014–2015 study period (out of 122 days (42.6%)), although detections at the main fishway entrance show that in MS1 and MS2 little migratory activity occurred in January and February anyway. During the second period the tile route was discontinuous and although lamprey could enter the tiles at the bottom, its efficacy was likely compromised. Indeed, no more lamprey were detected at either of the antennas located at the upstream exit of the fish pass after 18/12/2014. Thus, lamprey only ascended the fish pass in MS2 when tiles were in a continuous arrangement and all successful lamprey traversed the fish pass by using the tile-route. Increasingly, studded tiles are being installed on the downstream face of sloping weirs, an approach which has been laboratory-tested successfully for eel elvers (Vowles et al., 2015) and for river lamprey in the laboratory (A. Vowles, pers. comm.) with quite encouraging results. Similar

results were found during trials with these tiles for sea lamprey, on the River Mulkear, Ireland (R. Conchuir, pers. comm.) and in the laboratory (U. Reinhardt, pers. comm.). There is therefore a pressing need to carry out well-planned, quantitative trials of the efficacy of studded tiles mounted on sloping weir faces, and combination fish passes (as here) under field conditions. Bristle elver passes are unlikely to be effective for passing river lamprey, since pilot PIT telemetry studies at Buttercrambe have demonstrated low entry rates and zero passage (J. Tummers, unpublished data).

If unmodified and tile-modified Larinier SAB passes offer inadequate passage for river lamprey, what other fishway options are available? Nature-like and low-gradient vertical slot fish passes are more appropriate for providing passage for a range of riverine taxa, including lampreys (Rodríguez et al., 2006; Pratt et al., 2009; Noonan et al., 2012). In Germany, on the River Elbe, 88% of PIT tagged river lamprey used a double slot vertical fish pass with 0.10 m drops between 9 m long basins at a 1% slope, though the passage efficiency was not stated (Adam, 2012). Keefer et al. (2010) demonstrated that for Pacific lamprey, passage duration can be reduced and success rate can be increased, especially under high flow regimes, by removing or modifying vertical steps and other sharp-edged corners and by providing adequate attachment surfaces. Radio telemetry by Aronsuu et al. (2015) identified a passage efficiency of 100% ($n = 10$) of river lamprey through a nature-like fish ramp at a low-head weir, while none of these lamprey passed a SAB pass, located at the same site. High passage efficiencies through low to moderate gradient nature-like or rock-ramp fish passes can likely be explained by the abundance of sites suitable for oral disc attachment and heterogeneous hydrodynamics, facilitating their use by so lamprey. However, Bunt et al. (2012) documented the frequent occurrence of poor attraction efficiencies of nature-like fish passes because of low attraction flow or unsuitable siting of the fish pass. As with all fish passes, careful attention to site selection improves both fish attraction and passage.

Acknowledgements

We are grateful to George Winn-Darley and Greg McCormick for access to the site and to David Lindsay (EA) for provision of flow-gauging data. Sergio Silva was supported by the Fundación Pedro Barrié de la Maza postgraduate grant programme 2013. This project was a collaboration between Durham University and the EA, funded by both partners.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2016.02.046>.

References

- Aarestrup, K., Lucas, M.C., Hansen, J.A., 2003. Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecol. Freshw. Fish* 12, 160–168.
- Adam, B., 2012. Fish ladders on the River Elbe near Geesthacht. In: Gough, P., Philipsen, P., Schollemma, P.P., Wanningen, H. (Eds.), *From Sea to Source: International Guidance for the Restoration of Fish Migration Highways*. Regional Water Authority Hunze en Aas, AD Veendam, The Netherlands, pp. 214–217.
- Armstrong, G.S., Aprahamian, M.W., Fewings, G.A., Gough, P.J., Reader, N.A., Varallo, P.V., 2010. Environment Agency Fish Pass Manual: Guidance Notes on the Legislation, Selection and Approval of Fish Passes in England and Wales. Environment Agency, Rio House, Bristol, pp. 369 <http://publications.environment-agency.gov.uk>.
- Aronsuu, K., Marjomäki, T.J., Tuohino, J., Wennman, K., Vikström, R., Ojutkangas, E., 2015. Migratory behaviour and holding habitats of adult river lampreys (*Lampetra fluviatilis*) in two Finnish rivers. *Boreal Environ. Res.* 20, 120–144.

- Baras, E., Lucas, M.C., 2001. Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. *Ecohydrol. Hydrobiol.* 1, 291–304.
- Boon, P.J., 1988. The impact of river regulation on invertebrate communities in the UK. *Regul. River* 2, 389–409.
- Bracken, F.S.A., Hoelzel, A.R., Hume, J.B., Lucas, M.C., 2015. Contrasting population genetic structure among freshwater-resident and anadromous lampreys: the role of demographic history, differential dispersal, and anthropogenic barriers to movement. *Mol. Ecol.* 24, 1188–1204.
- Bunt, C.M., Castro-Santos, T., Haro, A., 2012. Performance of fish passage structures at upstream barriers to migration. *River Res. Applic.* 28, 457–478.
- Castro-Santos, T., Haro, A., Walk, S., 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. *Fish. Res.* 28, 253–261.
- Caudill, C.C., Daigle, W.R., Keefer, M.L., Boggs, C.T., Jepson, M.A., Burke, B.J., Zabel, R.W., Bjornn, T.C., Peery, C.A., 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Can. J. Fish. Aquat. Sci.* 64, 979–995.
- Clay, C.H., 1995. *Design of Fishways and Other Fish Facilities*, second ed. Lewis, Boca Raton.
- Close, D.A., Fitzpatrick, M.S., Li, H.W., 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries* 27, 19–25.
- Clough, S.C., Lee-Elliott, I.H., Turnpenny, A.W.H., Holden, S.D.J., Hinks, C., 2004. *Swimming Speeds in Fish: Phase 2 R&D Technical Report No. W2-026/TR3*. Environment Agency, Bristol, pp. 82.
- Cooke, S.J., Bunt, C.M., Hamilton, S.J., Jennings, C.A., Pearson, M.P., Cooperman, M.S., Markle, D.F., 2005. Threats conservation strategies, and prognosis for suckers (Catostomidae) in North America: insights from regional case studies of a diverse family of non-game fishes. *Biol. Conserv.* 121, 317–331.
- Cooke, S.J., Hinch, S.G., 2013. Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering science, and practice. *Ecol. Eng.* 58, 123–132.
- Cooke, S.J., Hinch, S.G., Lucas, M.C., Lutcvage, M., 2012. In: Zale, A.V., Parrish, D.L., Sutton, T.M., Bethesda, M.D. (Eds.), *Biotelemetry and biologging Fisheries Techniques*, 3rd edition. American Fisheries Society, pp. 819–860, 2013.
- Dekker, W., Pawson, M., Wickström, H., 2007. Is there more to eels than slime: an introduction to papers presented at the ICES theme session in September 2006. *ICES J. Mar. Sci.* 64, 1366–1367.
- EC, 1992. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Off. J. L206*, 7–50, 22/07/92.
- Feunteun, E., 2002. Management and restoration of European eel population (*Anguilla anguilla*): an impossible task. *Ecol. Eng.* 18, 575–591.
- Foulds, W.L., Lucas, M.C., 2013. Extreme inefficiency of two conventional: technical fishways used by European river lamprey (*Lampetra fluviatilis*). *Ecol. Eng.* 58, 423–433.
- Gaudron, S.M., Lucas, M.C., 2006. First evidence of attraction of adult river lamprey in the migratory phase to larval odour. *J. Fish Biol.* 68, 640–644.
- Goolish, E.M., 1989. The scaling of aerobic and anaerobic muscle power in rainbow trout (*Salmo gairdneri*). *J. Exp. Biol.* 147, 493–505.
- Gordon, E., Meentemeyer, R.K., 2006. Effects of dam operation and land use on stream channel morphology and riparian vegetation. *Geomorphology* 82, 412–429.
- Gough, P., Philipsen, P., Schollemma, P.P., Wanningen, H., 2012. *From Sea to Source: International Guidance for the Restoration of Fish Migration Highways*. Regional Water Authority Hunze en Aas, AD Veendam, The Netherlands.
- Gowans, A., Armstrong, J.D., Priede, I.G., 1999. Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. *J. Fish Biol.* 54, 713–726.
- Hardisty, M.W., 1986. *Lampetra fluviatilis* (Linnaeus, 1758). In: Holcik, J. (Ed.), *The Freshwater Fishes of Europe, Part I. Petromyzontiformes*, vol. 1. Aula-Verlag, Wiesbaden, pp. 249–278.
- Hunn, J.B., Youngs, W.D., 1980. Role of physical barriers in the control of sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 37, 2118–2122.
- Jang, M.-H., Lucas, M.C., 2005. Reproductive ecology of the river lamprey. *J. Fish. Biol.* 66, 499–512.
- Katopodis, C., Williams, J.G., 2011. The development of fish passage research in a historical context. *Ecol. Eng.* 48, 8–18.
- Keefer, M.L., Clabough, T.C., Jepson, M.A., Johnson, E.L., Boggs, C.T., Caudill, C.C., 2012. Adult Pacific lamprey passage: data synthesis and fishway improvement prioritization tools. In: Technical Report 2012-8. Prepared for: Department of Fish and Wildlife Sciences College of Natural Resources, University of Idaho.
- Keefer, M.L., Daigle, W.R., Peery, C.A., Pennington, H.T., Lee, S.R., Moser, M.L., 2010. Testing adult Pacific lamprey performance at structural challenges in fishways. *N. Am. J. Fish. Manag.* 30, 376–385.
- Keefer, M.L., Peery, C.A., Lee, S.R., Daigle, W.R., Johnson, E.C., Moser, M.L., 2011. Behaviour of adult Pacific lamprey in near field flow and fishway design experiments. *Fish. Manag. Ecol.* 18, 177–189.
- Kemp, P.S., 2012. Bridging the gap between fish behaviour: performance and hydro-dynamics: an ecohydraulics approach to fish passage research. *River Res. Appl.* 28, 403–406.
- Kemp, P.S., Russon, I.J., Vowles, A.S., Lucas, M.C., 2011. The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshoot and undershot weirs. *River Res. Appl.* 27, 488–498.
- Kemp, P.S., Tsuzaki, T., Moser, M.L., 2009. Linking behaviour and performance: intermittent locomotion in a climbing fish. *J. Zool.* 277, 171–178.
- Laine, A., Kamula, R., Hooli, J., 1998. Fish and lamprey passage in a combined Denil and vertical slot fishway. *Fish. Manag. Ecol.* 5, 31–44.
- Larinier, M., Marmulla, G., 2004. Fish passes: types, principles and geographical distribution—an overview. Bangkok, Thailand. RAP Publication 2004/17 In: Velcomme, R., Petr, T. (Eds.), *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries*, FAO Regional Office for Asia and the Pacific, vol. II, pp. 1–14.
- Larinier, M., Travade, F., Porcher, J.P., 2002. Fishways: biological basis, design criteria and monitoring. *Bull. Fr. Peche Piscic.* 364 (Suppl.), 208.
- Liao, J.C., 2007. A review of fish swimming mechanics and behavior in altered flows. *Phil. Trans. Royal Soc. London B: Biol. Sci.* 362, 1973–1993.
- Loge, F.J., Arkoosh, M.R., Ginn, T.R., Johnson, L.L., Collier, T.K., 2005. Impact of environmental stressors on the dynamics of disease transmission. *Environ. Sci. Technol.* 39, 7329–7336.
- Lucas, M.C., Baras, E., 2001. *Migration of Freshwater Fishes*. Blackwell Science, Oxford.
- Lucas, M.C., Frear, P.A., 1997. Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *J. Fish Biol.* 50, 382–396.
- Lucas, M.C., Mercer, T., Armstrong, J.D., McGinty, S., Rycroft, P., 1999. Use of a flat-bed passive integrated transponder antenna array to study the migration and behaviour of lowland river fishes at a fish pass. *Fish. Res.* 44, 183–191.
- Lucas, M.C., Mercer, T., McGinty, S., Armstrong, J.D., 2000. Development and evaluation of a flat-bed passive integrated transponder detection system for recording movement of lowland river fishes through a baffled pass. In: Moore, A., Russell, I. (Eds.), *Advances in Fish Telemetry*. CEFAS, Lowestoft, pp. 117–127.
- Lucas, M.C., Bubb, D.H., Jang, M., Ha, K., Masters, J.E.G., 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshw. Biol.* 54, 621–634.
- Mallen-Cooper, M., Stuart, I.G., 2007. Optimising Denil fishways for passage of small and large fishes. *Fish. Manag. Ecol.* 14, 61–71.
- Masters, J.E.G., Jang, M.-H., Ha, K., Bird, P.D., Frear, P.A., Lucas, M.C., 2006. The commercial exploitation of a protected anadromous species the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse north-east England. *Aquat. Conserv.* 16, 77–92.
- Mateus, C.S., Rodríguez-Muñoz, R., Quintella, B.R., Alves, M.J., Almeida, P., 2012. Lampreys of the Iberian Peninsula: distribution: population status and conservation. *Endang. Species Res.* 16, 183–198.
- McLaughlin, R.L., Porto, L., Noakes, D.L.G., Baylis, J.R., Carl, L.M., Dodd, H.R., Goldstein, J.D., Hayes, D.B., Randall, R.G., 2006. Effects of low-head barriers on stream fishes: taxonomic affiliations and morphological correlates of sensitive species. *Can. J. Fish. Aquat. Sci.* 63, 766–779.
- Mesa, M.G., Bayer, J.M., Seelye, J.G., 2003. Swimming performance and physiological responses to exhaustive exercise in radio-tagged and untagged Pacific lampreys. *Trans. Am. Fish. Soc.* 132, 483–492.
- Moser, M.L., Almeida, P.R., Kemp, P.S., Sorensen, P.W., 2015. Lamprey spawning migration. In: Docker, M. (Ed.), *Lampreys: Biology, Conservation and Control*, vol. 1. Springer, Dordrecht, pp. 215–252.
- Moser, M.L., Keefer, M.L., Pennington, H.T., Ogden, D.A., Simonson, J.E., 2011. Development of Pacific lamprey fishways at a hydropower dam. *Fish. Manage. Ecol.* 18, 190–200.
- Nelson, M.L., McMahonald, T.E., Thurow, R.F., 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. *Environ. Biol. Fish.* 64, 321–332.
- NERC, 2015. CEH Web, National River Flow Archive, Data 27041—Derwent at Buttercrambe (accessed March, 2015) <http://www.ceh.ac.uk/data/nrfa/data/time.series.html?27041>.
- Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 320, 405–408.
- Noonan, M.J., Grant, J.W.A., Jackson, C.D., 2012. A quantitative assessment of fish passage efficiency. *Fish. Fish.* 13, 450–464.
- Parasiewicz, P., Eberstaller, J., Weiss, S., Schmutz, S., 1998. Conceptual guidelines for nature-like bypass channels. In: Jungwirth, M., Schmutz, S., Weiss, S. (Eds.), *Fish Migration and Fish Bypasses*. Fishing News Books, Oxford, pp. 348–362.
- Peake, S., McKinley, R.S., Scruton, D.A., 1997. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *J. Fish Biol.* 51, 710–723.
- Pess, G.R., McHenry, M.L., Beechie, T.J., Davies, J., 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Sci.* 82, 72–90.
- Pratt, T.C., O'Connor, L.M., Hallett, A.G., McLaughlin, R.L., Katopodis, C., Hayes, D.B., Bergstedt, R.A., 2009. Balancing aquatic habitat fragmentation and control of invasive species: enhancing selective fish passage at sea lamprey control barriers. *Trans. Am. Fish. Soc.* 138, 652–665.
- Quintella, B.R., Andrade, N.O., Koed, A., Almeida, P.R., 2004. Behavioural patterns of sea lampreys' spawning migration through difficult passage areas, studied by electromyogram telemetry. *J. Fish Biol.* 65, 961–972.
- Reinhardt, U.G., Eidietis, L., Friedl, S.E., Moser, M.L., 2008. Pacific lamprey climbing behavior. *Can. J. Zool.* 86, 1264–1272.
- Renaud, C.B., 1997. Conservation status of Northern Hemisphere lampreys (Petromyzontidae). *J. Appl. Ichthyol.* 13, 143–148.
- Rieman, B.E., Beamesderfer, R.C., Vigg, S., Poe, T.P., 1991. Estimated loss of juvenile salmonids to predation by Northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Trans. Am. Fish. Soc.* 120, 448–458.
- Rodríguez, T.T., Agudo, J.P., Mosquera, L.P., González, E.P., 2006. Evaluating vertical-slot fishway designs in terms of fish swimming capabilities. *Ecol. Eng.* 27, 37–48.

- Russon, I.J., Kemp, P.S., 2011. Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*. *J. Fish Biol.* 78, 1965–1975.
- Russon, I.J., Kemp, P.S., Lucas, M.C., 2011. Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fish. Manag. Ecol.* 18, 201–210.
- Rustadbakken, A., L'Abée-Lund, J.H., Arnekleiv, J.V., Kraabøl, M., 2004. Reproductive migration of brown trout in a small Norwegian river studied by telemetry. *J. Fish Biol.* 64, 2–15.
- Sfakiotakis, M., Lane, D.M., Davies, B.C., 1999. Review of fish swimming modes for aquatic locomotion. *IEEE J. Oceanic Eng.* 24, 237–252.
- Sjöberg, K., 1980. Ecology of the European river lamprey (*Lampetra fluviatilis*) in northern Sweden. *Can. J. Fish. Aquat. Sci.* 37, 197–198.
- Solomon, D.J., Beach, M.H., 2004. Fish pass design for eel and elver (*Anguilla anguilla*). In: R&D Technical Report W2-070/TR1. Environment Agency, Bristol, pp. 92.
- Thiel, R., Winkler, H.M., Riel, P., Neumann, R., Gröhsler, T., Böttcher, U., Spratte, S., Hartmann, U., 2009. Endangered anadromous lampreys in the southern Baltic Sea: spatial distribution long-term trend, population status. *Endang. Species Res.* 8, 233–247.
- Tuunainen, P., Ikonen, E., Auvinen, H., 1980. Lampreys and lamprey fisheries in Finland. *Can. J. Fish. Aquat. Sci.* 37, 1953–1959.
- Videler, J., 1993. *Fish Swimming*. St. Edmundsbury Press, Bury St. Edmunds, Suffolk, UK.
- Vowles, A.S., 2012. Experimental Quantification of the Response of Fish to Conditions Associated with Low-head Hydropower and Fish Passage Facilities. PhD Thesis. University of Southampton.
- Vowles, A.S., Don, A.M., Karageorgopoulos, P., Worthington, T.A., Kemp, P.S., 2015. Efficiency of a dual density studded fish pass designed to mitigate for impeded upstream passage of juvenile European eels (*Anguilla anguilla*) at a model Crump weir. *Fish. Manage. Ecol.* 22, 307–316.
- Vrieze, L.A., Bergstedt, R.A., Sorensen, P.W., 2011. Olfactory-mediated stream-finding behavior of migratory adult sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 68, 523–533.
- Vrieze, L.A., Bjerselius, R., Sorensen, P.W., 2010. Importance of the olfactory sense to migratory sea lampreys *Petromyzon marinus* seeking riverine spawning habitat. *J. Fish Biol.* 76, 949–964.
- Wagner, C.M., Twohey, M.B., Fine, J.M., 2009. Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? *Anim. Behav.* 78, 593–599.
- 1980 Wardle, C.S., 1980. Effects of temperature on the maximum swimming speeds of fish. In: Ali, M.A. (Ed.), *Environmental Physiology of Fishes*. Plenum Publishing Corp, New York, pp. 519–531.
- Wilkie, M.P., Brobbel, M.A., Davidson, K., Forsyth, L., Tufts, B.L., 1997. Influences of temperature upon the post-exercise physiology of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 54, 503–511.
- Whitton, B.A., Lucas, M.C., 1997. Biology of the Humber rivers. *Sci. Total Environ.* 194–195, 247–262.
- Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., Travade, F., 2012. Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. *River Res. App.* 28, 407–417.
- World Commission on Dams, 2000. *Dams and Development, a New Framework for Decision-Making*. Earthscan Publications Ltd., London.
- Xu, K., Milliman, J.D., 2009. Seasonal variations of sediment discharge from the Yangtze River before and after impoundment of the Three Gorges Dam. *Geomorphology* 104, 276–283.
- Yoshiyama, R.M., Fisher, F.W., Moyle, P.B., 1998. Historical abundance and decline of Chinook salmon in the Central Valley region of California. *N. Am. J. Fish. Manag.* 18, 487–521.
- Zabel, R.W., Williams, J.G., 2002. Selective mortality in Chinook salmon: what is the role of human disturbance? *Ecol. Appl.* 12, 173–183.